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Development and Use of Matrix Models to Evaluate Alternative Management Approaches for Restoring Biological Populations

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The Problem

In the U.S., there are nearly one thousand species listed as endangered or threatened under the Endangered Species Act of 1973. Many marine organisms have declined, but documented extinctions are relatively rare (Sissenwine and Rosenberg 1993, NRC 1990). However, freshwater systems are at particular risk. While only 11-15 % of terrestrial vertebrates in the U.S. are classified as rare or extinct, 34% of freshwater fishes, 65% of crayfishes, and 75% of unionid mussels are now seriously threatened or extinct (Master 1990). Despite strong efforts to improve water quality, none of the 251 fishes listed as rare in 1979 were removed from the list in 1989, except via extinction (Williams et al. 1989). Major factors cited for these declines include habitat modification, effects of introduced species, chemical alteration of the habitat (including enrichment), hybridization, and overharvesting. Frequently, declines have been attributed to more than one cause (Williams et al. 1989).

The future of threatened aquatic populations depends upon effective management and recovery plans. Unfortunately, our knowledge of a threatened species' life history and of the potential costs and benefits of various management alternatives is extremely limited. In addition, research budgets are often limited and time to arrive at conclusions short. To manage effectively under these constraints, it is critical to evaluate the *relative* effectiveness of specific changes in vital rates (e.g., juvenile survival vs. fecundity) on population responses (e.g., population growth rate, abundance, or size/age structure), and the importance of uncertainty in our knowledge of these vital rates.

The philosophical basis for our approach dates to Thomas Chamberlain's (1890) paper on "The method of multiple working hypotheses." Most patterns in nature are driven by multiple mechanisms, not by single causative factors. Chamberlain (1890) proposed that we could more rapidly understand cause and effect by considering multiple hypotheses, including interacting effects, and then proposing experiments or observations which would allow us to narrow the list to those hypotheses most likely to produce the observed dynamics. In management of a threatened species, we can consider proposed management approaches as alternative hypotheses and evaluate which management alternatives appear most (or least) likely to enhance population recovery.

Matrix Modeling

One set of tools for enhancing decision making involves deterministic matrix modeling; this approach focuses on relative changes in population responses as certain parameters in the population model are changed. One commonly used population response is λ, the population growth rate. The growth rate λ is related to the intrinsic rate of increase r obtained for Lotka's equation $r = 1n\ \lambda$. Elasticity analyses can reveal how changes in age- or stage-specific vital rates (e.g. survival, growth, or fecundity) affect λ. We can apply this approach to determine: 1) which stage-specific vital rates are most critical to population growth; 2) which processes or life history stages should be the focus of conservation: 3) which of an array of management alternatives is most likely to produce the desired results; and 4) where to focus limited research efforts to refine parameters for future analyses (Schemske et al. 1994, Heppell et al. 1997). In models which incorporate density dependence or stochasticity, the sensitivity of other response variables (such as population size) to changes in vital rates can also be examined.

It is outside the scope of this paper to outline fully the techniques for matrix modeling and analysis, but this is fully reviewed elsewhere (Caswell 1989, McDonald and Caswell 1993, Heppell et al. 1997). Deterministic, linear models are relatively simple to produce, easy to interpret, and provide analytic rather than simulation results. With a matrix model, we calculate the proportion of individuals in an age or stage class in each time period, dependent on the survival and growth rates of individuals within each class and the fecundity of individuals in each class. A transition matrix contains one row and column for each age/stage class in the model, with each entry representing the probability of survival and transition to another stage or fecundity. Using techniques from linear algebra, we can estimate λ, the stable age/stage distribution, and the reproductive value of individuals in each age/stage class. This approach assumes all individuals within a class are identical and that vital rates do not change over time. Deterministic models cannot be used to estimate future population size (despite being called projection matrices) and are inappropriate for small or isolated populations that are subject to high demographic stochasticity.

Matrix models require less data than individual-based or stochastic models. For conservation managers, this can be an advantage, because data are too limited for most threatened species to use more complicated modeling approaches. To produce a simple matrix model, we need age/stage specific vital rates information, similar to that included in a typical life table. The simplest matrix model is age-based (Leslie 1945), where surviving individuals grow into the next age class at each time step. In stage-based models, surviving individuals may remain in a stage for one or more time steps before making the transition to another life stage (Crouse et al. 1987). Organisms with complex life histories may make transitions to a variety of life stages (Heppell et al. 1994).

The real utility of matrix models hinges on elasticity (= proportional sensitivity) analysis;

this analysis allows quantitative comparisons of the relative impact of model parameters on a population response which can be used to qualitatively compare management alternatives. Details of the methods for elasticity analysis are reviewed elsewhere (deKroon et al. 1986, Caswell 1989, Heppell et al. 1997). Elasticity analysis can help managers decide which life stages are in most need of protection and which model parameters need additional research (Schemske et al. 1994). If we can determine how a particular management proposal is likely to influence vital rates, we alter the particular vital rates in the model and examine projected population responses to each management alternative. The best use for this type of analysis is to eliminate management alternatives that are unlikely to lead to population recovery, as in the headstarting (i.e., captive rearing) of Kemp's ridley sea turtles (*Lepidochelys kempi*) (Heppell et al. 1996).

Case Studies

Loggerhead Sea Turtles (Caretta caretta)

We evaluated alternative management scenarios for threatened loggerhead sea turtles in the southeastern U.S. using matrix models (Crouse et al. 1987, Crowder et al. 1994). By the mid-1980s, beach monitoring and nest protection programs had documented: 1) dramatic declines in adult nesting females; 2) nest, egg, and hatchling losses to erosion and predation; and 3) carcasses of drowned adult and juvenile turtles often washed ashore (these were termed "strandings"). Incidental capture of turtles in fishing gear, particularly shrimp trawls, appeared to account for most (but not all) of the strandings (Henwood and Stuntz 1987). In response to large numbers of stranded turtles, the National Marine Fisheries Service (NMFS) developed turtle excluder devices (TEDs) which could be installed in trawl nets to reduce turtle mortality. As managers considered requiring the use of TEDs in shrimp trawls, they encountered substantial resistance. Nest protection did appear to enhance egg survival, allowing the release of more hatchlings, at a minimal socioeconomic cost. Should managers require a strongly resisted approach (TEDs) of a industry already in financial trouble or opt for increasing low cost and widely popular nest protection projects?

Crouse et al. (1987) produced the first population model for loggerhead sea turtles. Elasticity analyses of the matrix showed that survival in the three juvenile stages, particularly the large juvenile stage (50-80 cm carapace length), as the most important to determining future population growth. Coincidentally, this was also the size class most often stranded dead on beaches. The model also documented that even 100% survival of the egg/hatchling stage was unlikely to reverse current population declines. Crouse et al. (1987) did not advocate terminating nest protection projects, but noted that nest protection projects without concurrent reductions in juvenile mortality (through the use of TEDs or some other method) would likely be futile. Subsequently the National Academy of Sciences review panel recommended requiring TEDs "in most trawls at most times of year" (NRC 1990). Recent estimates of reductions in strandings due to TEDs (Crowder et al. 1995) appear to be sufficient to allow loggerhead recovery (Crowder et al 1994). However, it will be decades before we can be sure of the effects of current TED regulations, because only the nesting female populations are monitored and females first return to nest at 20-25 years of age.

Southern Appalachian Brook Trout (Salvelinus fontinalis)

Brook trout populations in the Southern Appalachians have declined in response to multiple anthropogenic effects including the introduction of an exotic salmonid (rainbow trout, *Oncorhynchus mykiss);* a decrease in pH (through acid deposition); an increase in siltation and allochthonous nutrients, and a decrease in shade (from road building and logging); and an increase in fishing pressure. We developed a population model based on a simple size-classified projection matrix to examine multiple anthropogenic effects and determine which factors are most (or least) important to population dynamics (Marschall and Crowder 1996). Density dependent survival was added to the model by multiplying the linear transition matrix by a second matrix with per capita survival probabilities on the diagonal entries; survival in the age 0 size classes depended on body size and number of age 0 fish (Marschall and Crowder 1995).

We evaluated the sensitivity of equilibrium population size and size-class structure to a variety of parameter perturbations (Marschall and Crowder 1996). Potential brook trout responses to rainbow trout include a decrease in survival rate of small fish, a change in density dependence in survival of small fish, and a decrease in growth rates of all sizes. When we included these responses in the population model, we found that population size tended to decrease with an increase in small fish growth rate (producing a population with fewer, but larger, fish). In addition, changes in the patterns of density-dependent survival also had a strong impact on both population size and size structure. Brook trout respond to decreases in pH with decreased growth rates in all size classes, decreased survival rates of small fish, and decreased egg-to-larva survival rates. This combination of effects, at magnitudes documented in laboratory experiments, had severe negative impacts on the modeled population. If siltation effects were severe, the extreme increase in egg-to-larva mortality could have strong negative effects on the population. However, even very strong increases in large fish mortality associated with sport harvesting were not likely to cause local extinction. In all of these cases, the interaction of drastic changes in population size structure with randomly occurring floods or droughts may lead to even stronger negative impacts than those predicted from the deterministic model.

Because these fish can reproduce at a small size, negative impacts on survival of the largest fish were not detrimental to the persistence of the population. Because survival of small juveniles is density dependent, even moderate decreases in survival in this stage had little effect on the ultimate population size. In general brook trout will respond most negatively to factors that decrease survival of large juveniles and small adults, and growth rates of small juveniles.

Finfish Bycatch in Trawl Fisheries

Bycatch is the incidental catch of non-target species that occurs to some extent in almost all commercial fisheries. In the U.S. shrimp trawl fishery, located in the estuarine, nearshore, and offshore waters of the Gulf of Mexico and the Atlantic Bight, bycatch comprises an average of 60-80% of the catch by weight. Shrimp trawl bycatch consists mainly of juvenile fishes and invertebrates, including species that are highly valued as adults in other commercial or recreational fisheries. Commercial and recreational fishermen, as well as conservationists, have demanded reductions in bycatch on the grounds that these fish are "wasted." In addition, commercial and recreational fishermen in other fisheries face increasingly strict regulations because of declining fish stocks, and these fishermen are unwilling to accept new restrictions unless the incidental mortality is also reduced. For harvested populations, managers would like to know the tradeoff between bycatch and catch in targeted fisheries. For example, how much potential catch is lost due to bycatch?

Recent stock assessments for valuable species such as red snapper *(Lutjanus campechanus)* and weakfish *(Cynoscion regalis)* have clearly indicated that bycatch mortality is a significant factor in the decline of these species (Powers et al. 1987, Goodyear 1990, Vaughan et al. 1991). Because the shrimp trawl fishery is the most valuable fishery in the southeast, efforts to reduce bycatch have chiefly been aimed at developing bycatch reduction devices (BRDs), modifications of trawl gear that allow fish to escape while retaining shrimp. But managers looking to reduce bycatch are faced with several questions concerning bycatch reduction, including: How much should bycatch be reduced? What increase in the abundance of adults will result from a given level of bycatch reduction? How important to the population is juvenile bycatch mortality compared to other factors such as harvesting of adults, pollution, or winter cold spells that affect growth or survival in other stages of life?

In an ongoing study, we are using matrix models to analyze the effects of bycatch on fish populations in the Gulf of Mexico, where shrimping effort is high and bycatch is an order of magnitude higher than elsewhere in the U.S. (Diamond et al. in prep.). We used Atlantic croaker *(Micropogonias undulatus)* as a representative of the estuarine-dependent species complex, which accounts for 80-90% of the commercial fishes landed in the southeastern U.S. To investigate the effects of bycatch, we are using our model to examine the effects of different levels of Atlantic croaker bycatch and adult mortality, corresponding to management strategies aimed at reducing bycatch, reducing the harvesting of adults, or both. We are also exploring which parameters have the greatest effect on population growth rates and on the number of adult fish. It is premature to report our results here, but suffice it to say that survival in the large juvenile stage, which is heavily impacted by bycatch, is a highly sensitive process, suggesting that bycatch reduction for finfish, like sea turtles, may have strong population level effects.

Discussion

Matrix models may prove to be useful tools to focus research and management efforts and to enhance recovery of threatened populations. Because many declining populations also have poorly known population dynamics, information is often too limited to employ more robust approaches, including stochastic matrix models or individual-based models, which can examine more directly the effects of demographic and environmental stochasticity. Our approach explicitly considers that population declines are often due to multiple factors, some of which managers can respond to and others to which they cannot. These factors can be combined to yield multiple working hypotheses (Chamberlain 1890) regarding causes of the decline. These causes impact different life stages and vital rates at different magnitudes. Matrix models provide a way to qualitatively compare the population-level effects of mitigation techniques that can influence stage-specific vital rates. This allows us to determine which of many proposed management approaches is most (or least) likely to contribute to population recovery.

Given the severe problems with threatened populations in aquatic ecosystems and the limited resources with which to address those problems, we recognize the need for a simple approach to address alternative management approaches and to focus critical research efforts. Like any simple approach, matrix modeling has real limitations. But often it provides a viable initial approach to the problem.

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